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Practical guidelines for modelling post-entry spread in invasion ecology

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Abstract

In this article we review a variety of methods to enable understanding and modelling the spread of a pest or pathogen post-entry. Building upon our experience of multidisciplinary research in this area, we propose practical guidelines and a framework for model development, to help with the application of mathematical modelling in the field of invasion ecology for post-entry spread. We evaluate the pros and cons of a range of methods, including references to examples of the methods in practice. We also show how issues of data deficiency and uncertainty can be addressed. The aim is to provide guidance to the reader on the most suitable elements to include in a model of post-entry dispersal in a risk assessment, under differing circumstances. We identify both the strengths and weaknesses of different methods and their application as part of a holistic, multidisciplinary approach to biosecurity research.

Keywords

Biosecurity, Dispersal, Migration, Modelling, Post-entry spread

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Introduction

Invasive species can have enormous economic and ecological impacts (Perrings et al. 2000, Pimentel 2011, Simberloff et al. 2005, Simberloff 2013). If we can assess the invasion threat early in the invasion process, we are likely to have more success in controlling the species, and suffer less impact than if we cannot. In general, the rate of spread of an invasive species will influence practical issues around our ability to control its spread and thus its ultimate impact. Targeted research to address the early, 'post-entry' stage of invasion is critical to inform management strategies and ultimately to improve biosecurity.

This article focuses on this 'post-entry spread' stage of the invasion process, specifically understanding dispersal processes and modelling the spread and establishment potential of a pest or pathogen once it has arrived into a region. We differentiate this from the population dynamics and dispersal of native species, as post-entry pest spread of non-native species has particular features that add to the modelling challenge. These include the requirement for rapid response, data paucity and high levels of uncertainty.

Whilst the majority of pest and pathogen entry today is largely due to anthropogenic pathways (Wilson et al. 2009), mainly from the transport of goods and commodities (Costello and McAusland 2003), once a pest has gained entry the mechanisms of spread can be multiple and diverse. The rate of spread will depend on a range of factors not just relating to the species' ecology but also relating to host distributions and to potential dispersal vectors; not only human but animal and environmental (such as wind or ocean currents). Ecological factors and landscape context may influence the pest/pathogen, vector and host, either facilitating or inhibiting the dispersal of the species. Likewise, the success of individual dispersal events may be strongly influenced by low probability extreme meteorological events, or by human-induced or other environmental factors.

When integrated with field-based research and surveillance, dispersal models can help inform pest and pathogen outbreak management about a range of processes, such as the rate of spread of a pest (Gilbert and Liebhold 2010), which can lead to better surveillance strategies (Cacho et al. 2010, Demon et al. 2011, Epanchin-Niell et al. 2012), and more effective response strategies (Coutts et al. 2011). Models can also be used to inform policy-makers about the risks posed to target ecosystems (Rutherford et al. 1999), at both immediate and long-term time scales (Kriticos et al. 2003; 2013a). Similarly, integration of dispersal simulation models and economic models can help to inform the design of optimal management strategies (Bogich et al. 2008, Carrasco et al. 2009, Florec et al. 2013, Kriticos et al. 2013b). For example, models can be used to decide when and at what scale a management strategy should be implemented given the progression of an invasion, and to decide whether the costs will outweigh the benefits.

With such diversity of pathways, scales and complexity of dispersal processes for post-entry spread, and with such a wide range of possible applications, there is a parallel diversity of modelling methods. We aim to give an overview here to help guide modellers to select appropriate methods.

Background

Models of pest and pathogen spread post-entry largely occupy one of two categories of model: analytical methods (Hastings 1996, Kot et al. 1996, Neubert and Caswell 2000, Royama 1992) and mechanistic, process-based methods (Higgins and Richardson 1996, Jongejans et al. 2008). Analytical models have been used for many years to study dispersal in ecology, beginning with simple diffusion equations (Skellam 1951). An analytical model can be broadly defined as a deterministic mathematical expression. Such models seek to distil the complexity of a system or process into a single representation of its behaviour under given circumstances. They have the advantage that they tend to be more easily generalised than mechanistic models (Turchin 1998). They incorporate a range of techniques, in particular theoretical or empirical curve fitting models for dispersal kernels and other generalisations of the movement of organisms as a simplified physical process (e.g. travelling wave (Sharov and Liebhold 1998), matrix models (Parker 2000) and diffusion (Kot et al. 1996)). Analytical models have varying data requirements, depending on whether they are developed as purely abstract theoretical models or if they are phenomenological statistical models that are empirically derived. In the latter case data availability often becomes a big issue for modelling incursions (see following section). Such methods generally involve assumptions that include uniformity of the landscape and population, which mean they are simple to implement but can be highly abstract. Criticisms of these models are a lack of complexity and realism that can be key to studying processes such as long-distance dispersal and the influence of landscape heterogeneity. Moreover, long-distance dispersal events are often caused by different mechanisms to short distance dispersal and are highly significant drivers of accelerated population spread (Liebhold and Tobin 2008).

To explore the long distance connectivity of populations, network models and metapopulation models have also been applied to invasion ecology in recent times (Chadès et al. 2011, Drake and Mandrak 2010, Facon and David 2006, Paini and Yemshanov 2012). Whilst these also have the advantage of simplifying complex processes, equally they make their own assumptions about the uniformity and 'patchiness' of the landscape.

Mechanistic, process-based simulation models are a more recent development for modelling spread post-entry (Turchin 1998), enabled in part by the growing power of computing to support large, complex models. Such approaches to dispersal modelling align with 'ballistic' simulations or in physics termed 'Lagrangian' models – where individual pathways are traced as they move according to a set of stochastic or behavioural rules (e.g. individuals influenced by wind trajectories). Such models tend to have greater flexibility across spatial scales, and therefore can more easily encompass both short and long distance dispersal events. Consequently, individual-based models (Grimm and Railsback 2005), cellular automata (Travis and Dytham 2002) and trajectory models (Chapman et al. 2010, Nathan et al. 2005) have become part of the ecological modeller's toolkit over the last few years, although there are relatively few

examples of the application of these methods to dispersal modelling for post-entry spread (e.g. Guichard et al. 2012, Kanarek et al. 2012).

It is also possible and can be advantageous for a dispersal model to contain both analytical and mechanistic components (e.g. Nathan et al. 2011). One example is WALD (Katul et al. 2005), which is used to estimate long distance dispersal kernels of wind-dispersed seeds and their escape probability from the plant canopy. A computationally intensive trajectory model that incorporates the effects of canopy turbulence was used to derive an expression for an analytical model, therefore retaining the mechanisms but giving the advantage of analytical simplicity (essentially an inverse Gaussian distribution). More broadly, bringing together the simplicity of an analytical, phenomenological method with mechanistic understanding of processes can be very powerful (e.g. Pitt et al. 2011).

Multiple dispersal vectors add extra layers of complexity (Buckley et al. 2006, Pitt et al. 2009). Many species have multiple dispersal pathways and these can be considered by the model(s), using an integrated multi-modelling method (Harwood et al. 2009).

In addition, species niche models can inform post-entry spread in multiple ways. Firstly, they can inform the total area that can potentially be invaded. This information can define the spatial bounds of the spread modelling, i.e., the model 'universe', for both simulation and analytical spread models. Alternatively, a niche model can be used to differentiate between different components of a heterogeneous landscape over which a species may spread, and this can be used by spatially-explicit dynamic dispersal models (e.g., Pitt et al. 2011).

When considering how best to apply these models, understanding the ecology and landscape factors relevant to the population dynamic and dispersal of a pest or pathogen species is critical. Often, not enough consideration is given to an organism's ecology and behaviour prior to developing a dispersal model, where population dynamics models are commonly separated from dispersal simulation. However, biological processes operating at different spatial and temporal scales are key drivers in the dispersal process, and ideally should be taken into account explicitly.

In selecting a model, there are also important characteristics to consider, such as the *sensitivity* of the model (the proportion of known spatio-temporal dispersal events modelled correctly) *versus* the *specificity* of the model (the proportion of unoccupied sites that are modelled correctly) (Fielding and Bell 1997, Pitt et al. 2011). Where spread models combine highly specific model realisations to create a probability surface for occupancy, they inevitably become less specific through time, eroding their usefulness for addressing long-term strategic questions (Pitt et al. 2011). A good example of the sensitivity-biased effects of applying a stochastic mechanistic modelling method to long-term dispersal scenarios is Robinet et al. (2009). In this paper, the spread of the pinewood nematode was simulated over 23 years in China. A probability surface of nematode presence was generated from a combination of 300 replicate simulations. The fit of the model was assessed by comparing how many of the known locations fell into cells with a positive modelled probability. This commonly applied method ignores the model specificity (the number of cells that had a positive modelled probability, but did not include any

reported infestations). As a guide for surveillance activities, poor model specificity could lead to much wasted effort, and for pest risk, an over-estimate of the potential impacts of the pest due to inappropriately high rates of spread. Therefore there is a need to critically consider this effect when developing a model of post-entry dispersal (Fletcher and Westcott 2013), perhaps limiting mechanistic models to short-term tactical applications such as informing regional pest management plans, including activities such as surveillance, eradication and containment strategies, and using far simpler spread models for strategic applications such as pest risk modelling (e.g. Kriticos et al. 2013b).

The post-entry spread modelling framework

Defining biosecurity objectives

The rate of spread of a pest or pathogen can affect the present value of its future economic and ecological impacts, taking into account the economic discount rate; all else being equal, a slower-spreading pest/pathogen is thought to have less potential future impact than a faster-spreading one. However, for terrestrial plants in particular, there may be a deceptive time lag between the arrival of the pest and the point at which the rate of spread begins to accelerate (Mack et al. 2000). Thus, shortly after establishment it can be difficult to discern a potential invasive from a non-invasive species. This may hamper our ability to model such cases accurately unless the potential drivers of both the lag phase and subsequent growth phase of spread are known. The rate of spread of a pest can also influence practical issues around our ability to control its spread (not necessarily a linear relationship), and the communication tactics employed (e.g. emphasising detection and slowing the spread, versus advising land managers about methods to control the pest once it arrives in an area) (Sharov and Liebhold 1998).

The International Standards for Phytosanitary Measures (FAO 2006) highlight various factors that are important to the estimation of the spread potential of an organism after establishment. These include the need for reliable biological information on pest occurrence, which can then be compared with the outbreak situation. Key considerations include:

- suitability of the natural and/or managed environment for natural spread of the pest,
- movement with commodities or conveyances,
- intended use of the commodity,
- potential vectors of the pest in the outbreak area,
- potential natural enemies of the pest in the outbreak area.

In this regard, we seek to estimate the potential extent of the endangered area, as well as the likely rate at which that area might become occupied by the organism. In the early stages of response it is important to assess the factors above as rapidly as possible, along with the route of introduction, the mechanisms of subsequent movement

and the shape of the natural dispersal kernel. Some factors will be easier to assess than others. While the potential extent can be estimated using niche modelling methods based on the organism's overseas distribution and where available knowledge of its ecology, simulating the organism's rate of spread relies on estimated spread rates, of which our knowledge is often poor. For example, use of Ripley's K-function or an O-ring analysis with available data (Wiegand and Moloney 2004) allows rapid estimation of the likely points of introduction and spatial clustering by statistically analysing and describing aggregation or dispersion patterns up to or at a given distance from a source. However, many of the other parameters required for a full assessment of spread potential may not be estimated readily until after several months of research.

Post-entry spread models: from the conceptual to the mathematical

A framework is suggested for post-entry dispersal modelling (Fig. 1). We expand on the key aspects of this framework in the following sections. Important to this process are clearly defined biosecurity objectives and scale informing the conceptual model (1), with an awareness of the constraints (such as time and the value of the problem in terms of pest/pathogen impact). Two primary issues are faced when modelling post-entry spread: obtaining data for model parameterisation and the difficulty of modelling multiple dispersal pathways (Pitt et al. 2009). Data availability can be a limiting factor in post-entry dispersal modelling, thus a consideration of what data is available is critical at the conceptual stage. Data availability may constrain how the model can be calibrated (3) or evaluated once the model is developed, which will affect the reliability of the model results (4). In addition, at the model refinement stage (3 and 4), the modeller may also include other methods with which to refine a model, such as Bayesian learning, and also validate the model, if appropriate data is available. In addition, an estimation of model uncertainty is an important basis for reliable decision making.

In the model formulation (2), a consideration of *scale* and *complexity* is paramount. How complex can the model be, given the availability of data and knowledge of the system, and how complex does the model need to be to address the salient questions? In general the complexity of a model is determined by the model scope and purpose, and the complexity of the study system. However, in rapid response situations, the inevitable lack of data means that in general it is best to construct simple (perhaps over-simplified) models rather than complex models (Jørgensen and Bendoricchio 2001). This may mean that species-specific models require rapid construction or that general model (e.g. traits-based or 'meta-models') may be applied in a specific incursion context (Saltelli et al. 2008). An advantage of simpler models is their more rapid generalisation to future contexts defined by new invasive species and landscapes, though it is important that such models balance generality with a need to include important processes at a sufficient level of mechanistic realism (Renton et al. 2011, Savage et al. in press).

As more data becomes available, model complexity and specificity can be increased. When selecting a modelling method, we suggest that modellers should con-

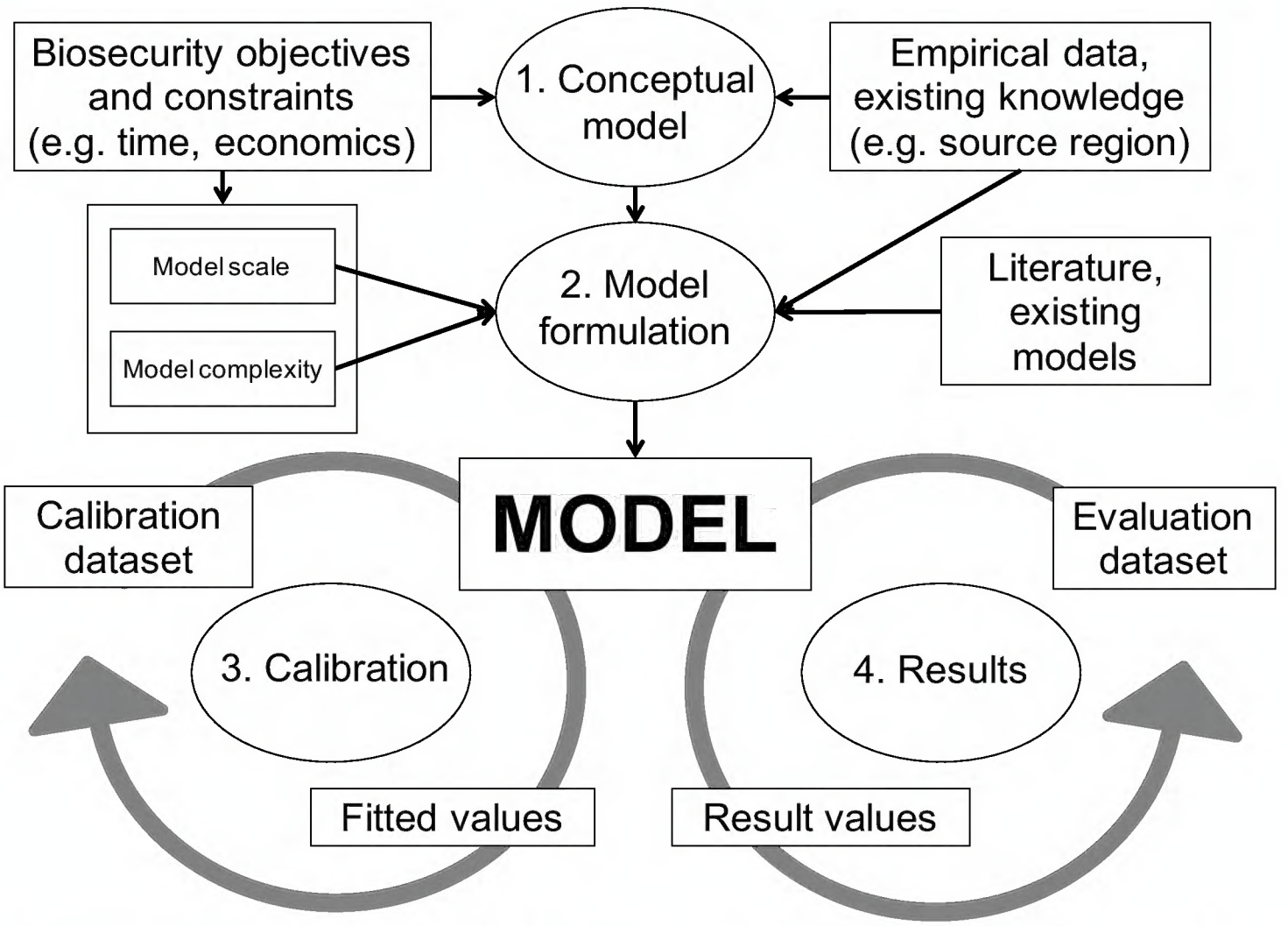

Figure 1. A framework for the model building process, when two data sets are available – one for fitting and one for evaluating the model (after Guisan and Zimmermann 2000).

sider a) the minimum level of model complexity required to address the pressing and foreseeable management and research questions, and b) the maximum level of model complexity that can be supported by the available knowledge and resources. Where a < b, the modeller has the option of choosing to build an elaborate model, perhaps capable of addressing unthought-of questions. Where a > b there is an information deficit and decision-makers expectations and confidence in the model results may need to be managed carefully. For pre-border risk assessments, there is latent demand for spatially-explicit spread models that are combined with impacts. Unfortunately, the initialisation of such models is a critically sensitive factor. Prior to an incursion and establishment of a pest or pathogen, the starting point for the spread model is unknown, and unknowable, a situation similar to that of the state of Schrödinger's Cat prior to opening the box.

The importance of scale

Temporal and spatial scale has an important role in the modelling process. Models for invasion post-entry pest spread most often need to be spatially-explicit, as landscape structure can impact on the invasion process significantly (With 2002) and policy-

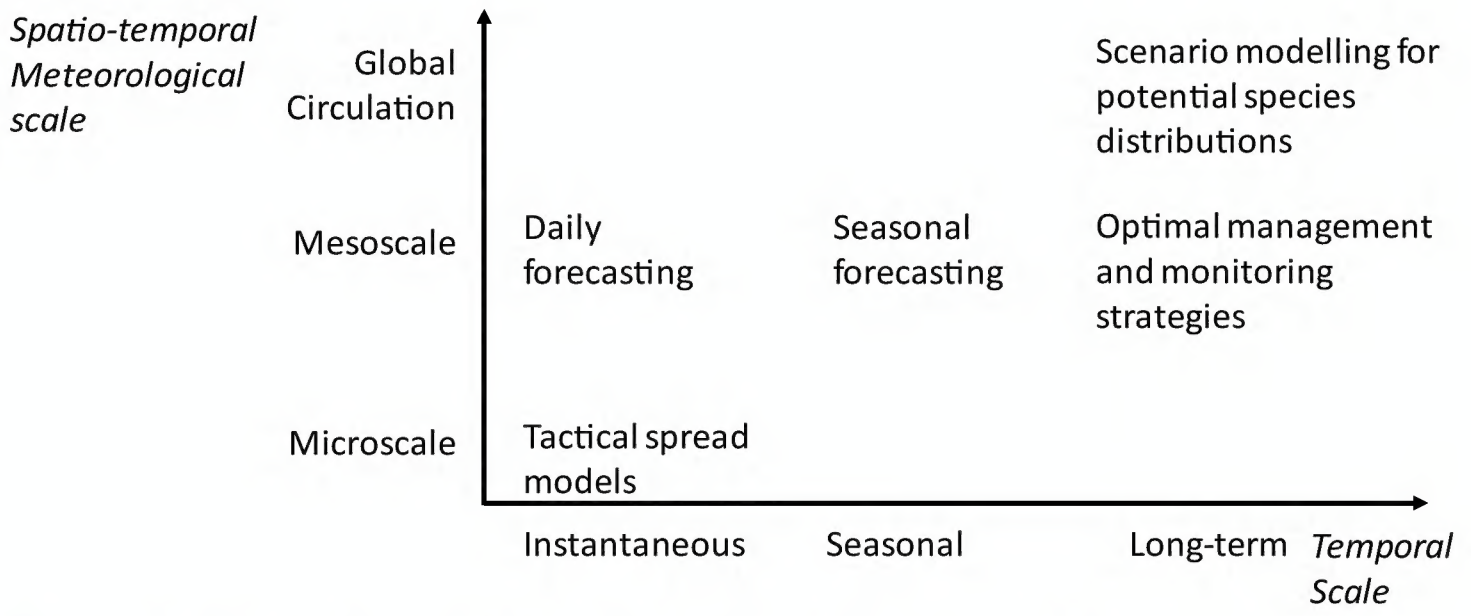

Figure 2. Pest and pathogen modelling foci at different spatio-temporal scales.

makers generally consider both pest-led and site-led management strategies. This allows models to inform spatial contingency planning to control or manage an outbreak. Some policy relevant applications outlined in the introduction are more relevant at particular landscape scales than others, or may be answered in different ways depending on the scale of the model. For example, there are five different kinds of model that are developed for post-entry spread of pests or pathogens to address policy relevant issues: tactical spread models, daily forecasting, seasonal forecasting, optimal management and monitoring strategies, and scenario modelling for future species distributions. The different focuses of the models result in them operating at different spatial-temporal scales (Fig. 2). Models that operate on a 'short-term' timescale, i.e. days to months, tend to also focus at a local spatial scale close to an outbreak, to consider issues of tactical spread and daily or seasonal forecasting. 'Long-term' models, i.e. operating across years to decades, tend to operate at much larger spatial scales to consider future species distributions and long-term management or monitoring strategies.

Although operating at different spatio-temporal scales, all of these models are likely to be required as soon as possible in a biological invasion. For example, long-term pest risk assessments are critical to help evaluate the suitable level of response to the incursion, e.g. through an economic analysis (e.g. Bogich et al. 2008, Carrasco et al. 2009, Kriticos et al. 2013b). Scenario models may also be constructed that allow for the user to explore potential invasion pathways, rate of spread and locations at risk (e.g. Harwood et al. 2009). These all require a certain capacity to simulate the movement and timing of pest outbreaks following the initial establishment.

A methodological roadmap

To summarise the broad range of methods that are available to modellers, we have identified important attributes of each of the model types that are commonly used to simulate post-entry spread (Table 1). For each of these methods, we highlight the common model

Table 1. Summary of model types and characteristics commonly used in post-entry pest and pathogen modelling, including examples and key references.

Model Type	Spatially implicit	Dispersal Kernels	Individual-based models	Cellular Automata	Gaussian Plumes	Trajectory models	Network models and Metapopulation models	Potential distribution models
Common model focus (see also Fig. 2)	Tactical spread	Tactical spread; Daily forecasting	Tactical spread; Daily forecasting	Seasonal forecasting	Tactical spread; Daily forecasting	Seasonal forecasting; Scenario modelling for future distributions	Seasonal forecasting; Scenario modelling for future distributions	Potential distribution, identifying the assets at risk, providing a forcing function for the rate of spread across heterogeneous landscapes, Scenario modelling for future distributions
Common model spatial scale (micro, meso, global circulation)	Mesoscale	Microscale; Mesoscale	Microscale; Mesoscale	Mesoscale	Mesoscale; Global circulation	Mesoscale; Global circulation	Mesoscale; Global circulation	Mesoscale; Global circulation
Common model temporal scale (instantaneous, seasonal, long-term)	Seasonal; long-term	Instantaneous	Instantaneous; Seasonal	Seasonal	Seasonal; long-term	Seasonal; long-term	Seasonal; long-term	long-term
Category (analytical or mechanistic)	Analytical	Analytical	Mechanistic	Mechanistic	Analytical	Mechanistic	Analytical	Analytical (majority), but some can be mechanistic or semi-mechanistic.
General pest / pathogen characteristics	Passive movement; Single dispersal event	Passive movement; Single dispersal event	Any mobile organism	Any mobile organism	Passive movement; Single dispersal event	Any mobile organism	Population contained within a clearly identifiable area/habitat. Specialists.	Any organism. Works best with sessile organisms, though some models can accommodate mobile organisms.
Common data requirements	Pest source; Dispersal rate; Population density	Population density; Dispersal distance; Dispersal rate; Wind speed and direction; Pest source.	Individual life-history; Behavioural rules (including dispersal); Pest source; Landscape data (e.g. land use, habitat suitability etc).	Dispersal distance; Dispersal rate; Wind speed and direction; Pest source; Pest population dynamics; Landscape data (e.g. land use, habitat suitability etc).	Pest source; Wind speed and direction; Dispersal rate; Population density	Pest source; Multi-level wind field data; Elevation; Pest dispersal ecology and survival;	Habitat patches; Population dynamics; Population density; Dispersal rate (between patches); 'connectivity' and 'travel cost' between patches.	Well known pest distribution at least in native range (presence and absence) and ideally some information on introduced range; constraints on pest survival and population growth

Model Type	Spatially implicit	Dispersal Kernels	Individual-based models	Cellular Automata	Gaussian Plumes	Trajectory models	Network models and Metapopulation models	Potential distribution models
Invasion ecology examples	Waage et al. (2005)	Carrasco et al. (2010), García Adeva et al. (2012), Harwood et al. (2011) , Lindstrom et al. (2011), Savage et al. (2011)	Higgins et al. (1996), Higgins and Richardson (1998), Nehrbass et al. (2007), Nehrbass and Winkler (2007), Murphy et al. (2008), Rutherford et al. (1999)	Kawasaki et al. (2006), Merow et al. (2011), van Dorp et al. (1997)	Monty et al. (2008), Skelsey et al. (2010)	Deveson et al. (2005), Hopkinson and Soroka (2010), Rochester et al. (1996), See and Feist (2010)	Chadès et al. (2011), Drake and Mandrak (2010), Facon and David (2006)	Kriticos et al. (2003), Yonow and Sutherst (1998);
Key References	Shigesada and Kawasaki (1997)	Greene and Calogeropoulos (2002), Kot et al. (1996), Skellam (1951)	Grimm and Railsback (2005)	Travis and Dytham (2002), von Neumann (1951), Wolfram (1983)	Overcamp (1976)	Scott and Achtemeier (1987), Nathan et al.(2005), Kunz et al. (2008)	Hanski (1999), Moslonka-Lefebvre et al. (2011)	Elith and Leathwick (2009), Elith et al. (2010), Kriticos and Randall (2001), Sutherst and Bourne (2009), Webber et al. (2011)
Advantage	Minimal data requirements.	Minimal data requirements.	Accounts for environmental heterogeneity; Emergence; Flexibility; Scale free.	Accounts for environmental heterogeneity; Less computationally and data intensive than fully individual-based models.	An analytical simplification of atmospheric complexity; minimal data requirements.	Incorporates atmospheric or oceanic processes; Can account for landscape effects (e.g. roughness, elevation);	Relatively simple; Allows examination of important processes including connectivity and flow at multiple scales.	Long-term risks; incorporates environmental change; large scale.
Disadvantage	Highly simplistic; assumes uniform landscape; May not be biologically realistic.	Often assumes uniform landscape; Relatively simplistic treatment of dispersal; May not be biologically realistic.	Complexity; data intensive; Species specific	data intensive; Strong influence of grid cell size and shape on dispersal; Relatively simplistic treatment of dispersal.	Assumes uniform landscape;	Complexity; data intensive	Assumes clearly defined habitat patches; complete knowledge of 'empty' and 'occupied' sites; Relatively simplistic treatment of dispersal.	Ignores evolutionary change; Scale specific.

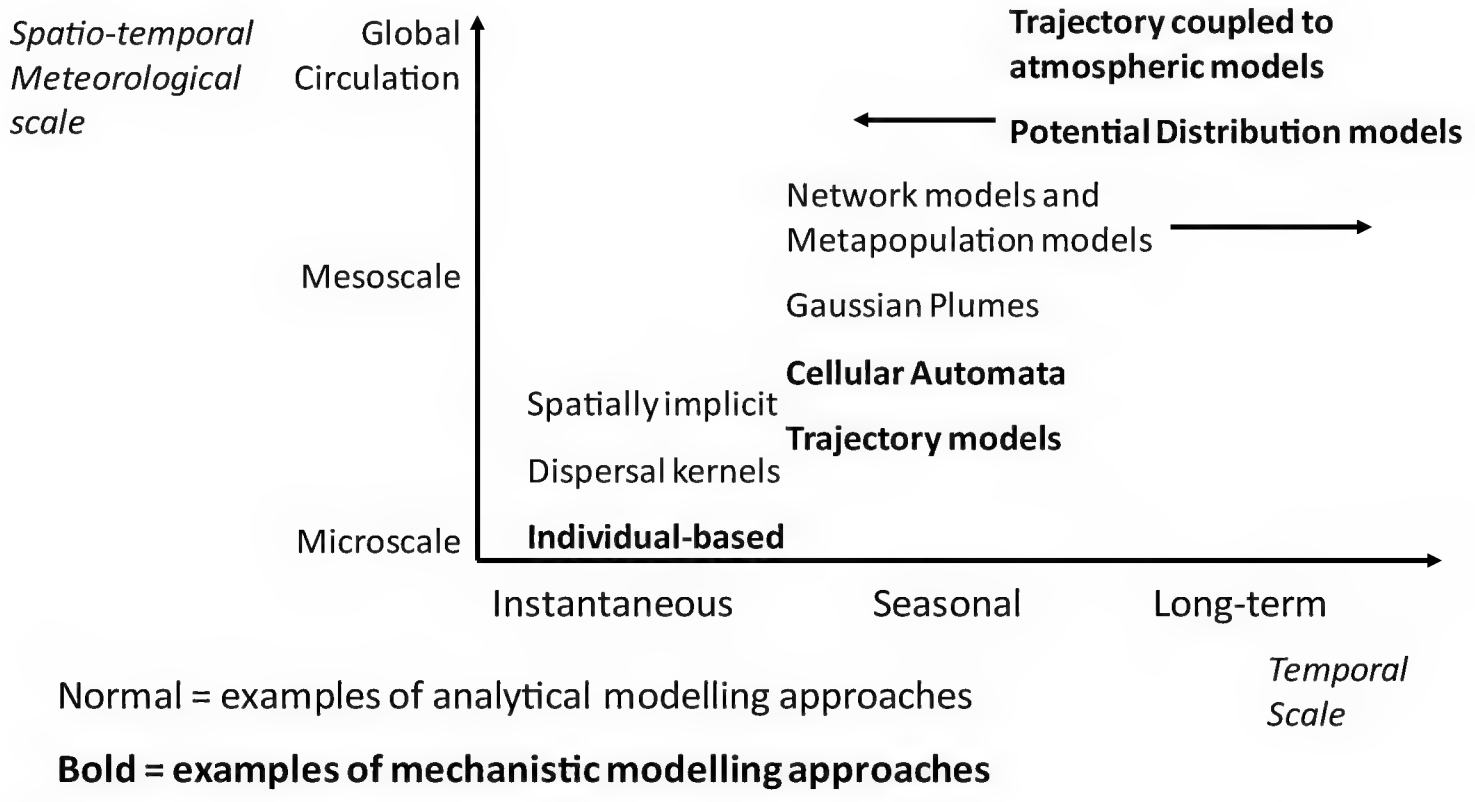

Figure 3. Examples of dispersal modelling techniques employed at different spatio-temporal scales.

focus and application, with references to some key examples in the literature. We identify the common data requirements, and highlight the overall advantages and disadvantages of each method. We also categorise the models according to their most appropriate temporal and spatial scale of use (although we acknowledge there is some potential overlap between our categories and that our references may refer to more than one scale or approach).

By understanding the scale at which policy questions are formulated (Fig. 2), we can align the spatio-temporal scale at which particular modelling techniques are best applied (Fig. 3) to identify which modelling methods may be best to use for particular policy questions (Table 1). However, it should be noted that in many cases it is necessary to examine an incursion event at multiple spatial and temporal scales and there can be significant advantages in doing so, such as an increased understanding of the invasion process and accounting for non-equilibrium of the species with the environment (Jones et al. 2010). This means that the modeller may need to select a flexible modelling approach that can span multiple spatial scales (see Table 1), or it may be necessary to develop multiple, possibly integrated models to address the range of dispersal pathways or policy questions that are posed. To further illustrate the pathway the modeller may take to arrive at using a particular modelling approach (or approaches) to address a particular problem, we have condensed the above to a flow-diagram (Fig. 4). This is intended as a further guide and illustration of the concepts in this paper. Constraints dictate the type of model and level of complexity that can be achieved, in relation to a biosecurity objective. In particular, the complexity of a model will be constrained by the available knowledge about the organism and it's behaviour, that may lead to assumptions about the organism. Constraints may also relate to the level of complexity and capacity for model development. It may be that to achieve an appropriate model, constraints must be overcome as there is no other option.

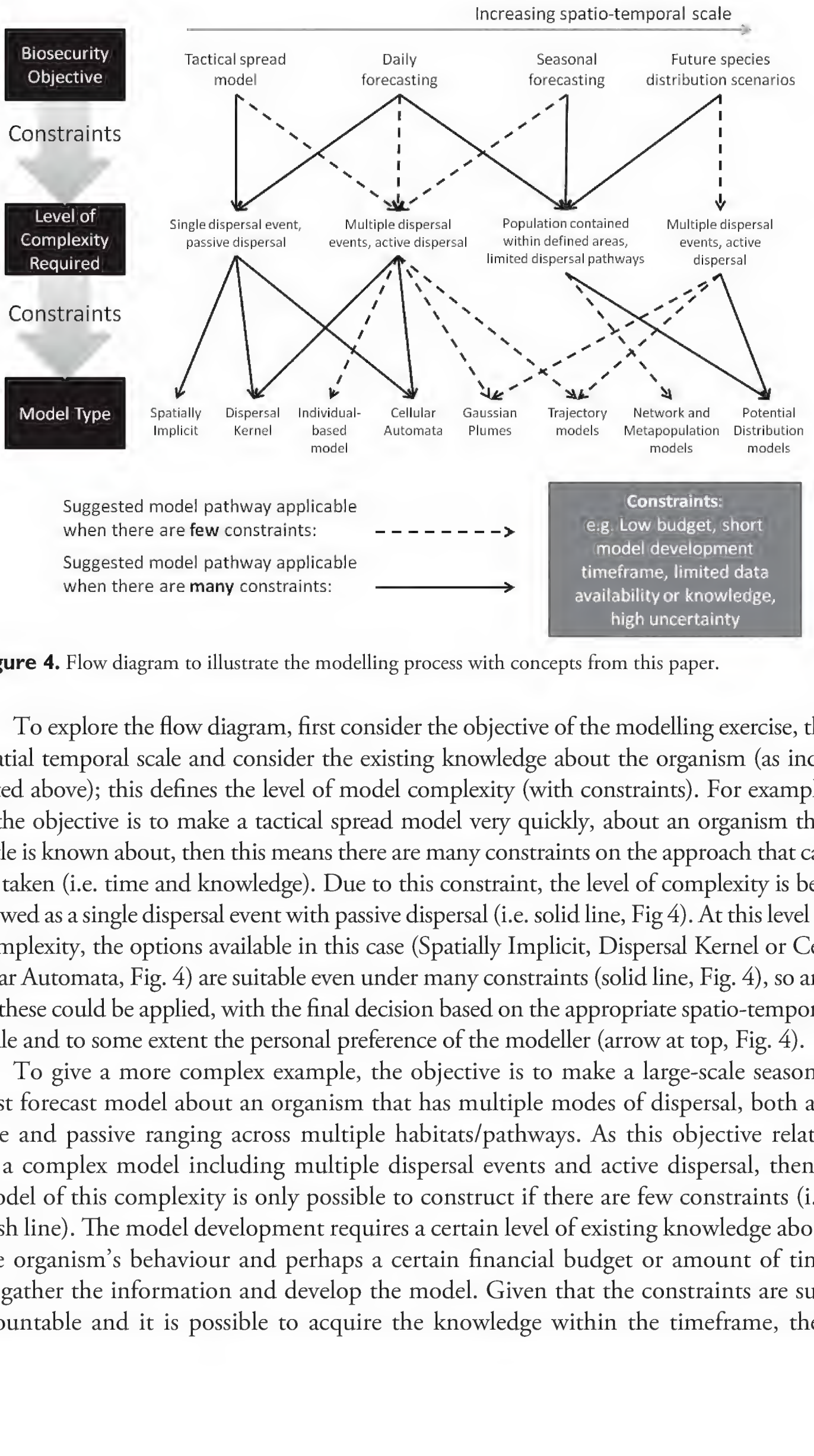

Figure 4. Flow diagram to illustrate the modelling process with concepts from this paper.

To explore the flow diagram, first consider the objective of the modelling exercise, the spatial temporal scale and consider the existing knowledge about the organism (as indicated above); this defines the level of model complexity (with constraints). For example, if the objective is to make a tactical spread model very quickly, about an organism that little is known about, then this means there are many constraints on the approach that can be taken (i.e. time and knowledge). Due to this constraint, the level of complexity is best viewed as a single dispersal event with passive dispersal (i.e. solid line, Fig 4). At this level of complexity, the options available in this case (Spatially Implicit, Dispersal Kernel or Cellular Automata, Fig. 4) are suitable even under many constraints (solid line, Fig. 4), so any of these could be applied, with the final decision based on the appropriate spatio-temporal scale and to some extent the personal preference of the modeller (arrow at top, Fig. 4).

To give a more complex example, the objective is to make a large-scale seasonal pest forecast model about an organism that has multiple modes of dispersal, both active and passive ranging across multiple habitats/pathways. As this objective relates to a complex model including multiple dispersal events and active dispersal, then a model of this complexity is only possible to construct if there are few constraints (i.e. dash line). The model development requires a certain level of existing knowledge about the organism's behaviour and perhaps a certain financial budget or amount of time to gather the information and develop the model. Given that the constraints are surmountable and it is possible to acquire the knowledge within the timeframe, then

different model types might be chosen, again relating to further constraints on model complexity/development such as budget/time: (1) if there are many constraints at this point the suggestion is the use of dispersal kernels or cellular automata – which simplify the known complexity of the dispersal events and mechanisms, or (2) if there are few constraints then a mechanistic approach may be taken such as individual-based modelling, gaussian plumes or trajectory models, all of which can better represent the complexity of the dispersal mechanisms. The other option for seasonal pest forecasting, if the first constraint cannot be met (i.e. the modeller is required to assume highly simplified behaviour such as limited dispersal pathways within defined areas), then the modeller can make the assumption of a more limited mode of dispersal that allows for such constraints. This leads to a different approach where the preferred option (if there are further constraints relating to e.g. model development time and budget) would be potential distribution models; however if a more dynamic approach is feasible by fewer constraints at this point (e.g. as there is good data availability about movement pathways) then network models/metapopulation models may be more appropriate.

Data availability

The importance of integrating field-based research and surveillance efforts with models as part of an ongoing multidisciplinary research effort continues to be highlighted in the literature (Restif et al. 2012). Ideally, a library of observed spread rates can provide valuable parameterisation for models, whilst at the same time models may inform ongoing surveillance efforts (e.g. Leighton et al. 2012, Leskinen et al. 2011, Fletcher and Westcott 2013). However, in practice good data are rarely available for post-entry spread modelling. Surveillance efforts may be *ad hoc*, and therefore not provide full coverage of the range and dispersal rate of the pest or pathogen as the invasion front moves. This is especially the case if the intrinsic probability of detecting an organism when present is low, given the existing surveillance technologies. Indeed, it is the estimated capacity for dispersal that will greatly influence the modelled rate of spread of the organism. For example, leptokurtic dispersal kernels (i.e. fat tailed compared to a normal distribution) lead to accelerating rates of population spread (Shigesada et al. 1995). While the extreme "fat tailed" dispersal events can have the largest influence on the overall behaviour of a dispersal model, it is these extreme events that are the most difficult to observe, and hence to estimate their prevalence. Even if good spread rate data are available on the characteristics of a species in another invaded range, this may not transfer into the context of a new region due to differences in natural and anthropogenic conditions. Models must therefore be constructed with an awareness of the shortcomings of data availability and the impact this will have on the model results, including presence-only data, bias to particular regions, missing life-history parameters and habitat suitability information.

Dispersal data are amongst the most difficult to collect and interpret. *Post-hoc* inferential methods relying on date-stamped geographical location records for invasions may be biased, incomplete and collected at a scale that is poorly suited for spread

modelling (Pitt et al. 2011), and there are few published examples of validated models derived from this source. Direct observations of spread rates are typically confounded by multiple potential sources of dispersers. Battisti et al. (2006) observed and measured an unusually rapid range expansion of winter pine processionary moth in its native range related to climate change, which was subsequently used to inform a simple spread simulation model for the invasion of New Zealand (Kriticos et al. 2013a).

Observations of the movement of an individual may have little informative value for the spread of a population. Spread rates for a species may vary greatly in relation to the potential movement of individuals, depending upon the suitability of the environment for population establishment and growth (Waage et al. 2005). Finally, there may be multiple dispersal pathways and therefore spread rates for a single organism: natural means of spread (e.g. wind dispersal) are often combined with long-distance transportation by humans or other animals (Harwood et al. 2009, 2011).

A key data requirement common for many models is to identify the incursion source. This underlines the importance of studies and models to identify entry points. However, even this may not be readily identifiable, and modellers must often work with partial information on an already spreading population without knowing the precise origin. Next, information on dispersal, such as movement rates, distances and directions are required. In more mechanistic methods, population dynamics and life-history parameters are required in order to simulate how individual dispersal events arise from a population. Habitat suitability and landscape data are also highly important in mechanistic, spatially-explicit simulations. A mechanistic method allows us to include important landscape interactions, such as foraging for food and breeding hosts, which can be critical factors of spread. This is one of the major advantages of a mechanistic method over an analytical one, as we are rarely able to adequately use an analytical approach to include the interaction of the organism with the landscape.

Ongoing monitoring and data acquisition is one solution to providing modelling support for decision-making in the face of knowledge scarcity. Existing models may be updated by calibration to fit new data as it is acquired, for example using methods such as a Kalman filter (most commonly used to update state-space equation model estimations with newly observed values, e.g. Hlasny 2011), allowing for more accurate short-term projections. However, the utility of the calibrated model estimates for a long term strategy is potentially compromised, as the underlying mechanism of population growth and dispersal can be mis-specified (e.g. Hooten and Wikle 2008). Thus, model reformulation and/or re-estimation is generally the most robust means to incorporate new data when the new data justifies it (Fig. 1).

Integrating existing knowledge and handling uncertainty

Knowledge gaps may relate to either a gap in knowledge of how a process is understood and therefore modelled (i.e. model uncertainty), or the uncertainty with which we can estimate the true value of a model parameter (parametric uncertainty). If the

knowledge of a critical process is incomplete, it is prudent to be cautious, and to be wary of management imperatives derived from regression-based patterns. The method of multiple competing hypotheses (Chamberlin 1890, Hilborn and Mangel 1997) is starting to gain popular acceptance as a basis for both studying and communicating deep uncertainty in areas as diverse as ecology and intelligence (Beven et al. 2005). An adaptive management, monitoring and modelling framework (A3MF) may be an appropriate method to adopt. In A3MF a model is iteratively updated as new knowledge or data is acquired that shows the model fails to represent the ecological process well (Holling 1978). Potential also exists within A3MF to employ different management strategies in different regions or periods of time to observe the response of the invasive organism to the different strategies and contexts, thereby accelerating our acquisition of knowledge about the organism and its management. However, A3MF requires long-term investment by a team of experts and managers over a time scale akin to the time scales of the invasion process, and the lagged impacts the invasion may have on the invaded agricultural or ecological system. This weakness of A3MF in its fullest sense is one of the reasons why simple, readily applied models have such broad appeal.

Parameter uncertainty, as a knowledge gap, is a function of data paucity and the availability of statistical methods. Model complexity also contributes to parameter uncertainty. On the one hand, highly complex models may contain so many parameters that not all may be known adequately, but on the other hand models that are very simple often contain parameters that are hard to estimate. Commonly, individual parameters are estimated through monitoring or experimental data targeted towards those parameters. These parameter estimates are then used in the model. If uncertainty in the estimates is quantified then the parameter uncertainty can be fed through the model to provide an estimate of parameter sensitivity. Other sources of uncertainty can also be incorporated into models through developing Bayesian posterior confidence intervals, such as measurement error or errors assigned to *ad hoc* parameter values (Higgins et al. 2003). In general, Bayesian methods have improved greatly with recent advances in computing, and can support a direct fitting of the model to the data, rather than a parameter plug-in approach. Hierarchical Bayesian methods of inference enable population dispersal models to be fitted to the data (Hooten and Wikle 2008, Royle et al. 2007). In lieu of a direct model-fitting procedure such as Hierarchical Bayes then the *ad hoc* 'plug-in' methods of model calibration are required, which may include:

1. garnering parameter values from analyses of the existing literature; or
2. minimising some measure of discrepancy between model output and the limited set of observations available, and which includes Approximate Bayesian Computation (ABC; Marjoram et al. 2003) and the inverse model problem.

Simulation is perhaps the best way to assign 'prediction' error or intervals to deterministic models, given uncertain starting conditions of the pest/pathogen population. Posterior prediction intervals can also be derived for stochastic models through cross-validation, and more generally through the use of independent test and training data sets. Generating

prediction intervals to be tested against new data sets also falls under the rubric of model validation (e.g. Higgins et al. 2001), which should also include logical tests for the "reasonableness" of model results. If model uncertainty of various management options on the end point of the invasion can be specified then a measure of policy or management activity risk can be developed, which may help determine an optimal risk mitigation strategy.

Common to all dynamic models is a temporal limit in quantifying model error. In this case an error is associated with a single time step, and in iteratively running a model then the error is compounded. The consequence of this compounding error is that long term utility of any dispersal model is dogged by severe and growing uncertainty. Two options are then available: (i) continual updating of results by resetting the model's initial conditions to the current conditions (e.g., the Kalman Filter process); or (ii) applying a decision method developed for severe uncertainty. Continual updating is consistent with both A3MF and Bayesian model updating, or 'learning': as new data arrive then our understanding of the processes, our ability to predict system processes, or belief in our model should also improve. However, continual updating requires ongoing monitoring to feed the model any change in system state as it occurs. Continual updating is most appropriate for developing tactical management responses to invasions, but does nothing to address the inability of these models to address strategic questions in a timely manner.

In contrast, decision making under severe uncertainty is common for long-term strategy development, or where continual updating is a cost-prohibitive option. Several analytical decision frameworks have been developed for dealing with severe uncertainty, with the two most popular being robust optimisation (RO) (Ben-Tal et al. 2009, Hansen and Sargent 2007) and info-gap theory (IGT) (Yakov 2006). The key difference between the two methods is that IGT provides a robust decision only in the local neighbourhood of the best guess parameter value for a model, whereas RO provides a solution that is robust over the entire range of parameter values to worst case scenarios (Sniedovich 2010). Neither framework handles a multivariate decision and parameter space well. A conservative strategy is to limit decision frameworks under severe uncertainty to those few key parameters that contribute most to the variability in model output, as identified through a sensitivity analysis.

Discussion

There is no single recipe for constructing a model of post-entry spread, due the diversity of policy applications, ecological and landscape contexts, temporal and spatial scales and possible techniques to employ. We have attempted to present some practical guidelines on how to approach model framing and construction for post-entry spread in invasion ecology by identifying what method may be most suitable to apply to particular policy questions, at what spatial and temporal scale, given the available data and knowledge. In recent years, we have seen the evolution of more process-based, mechanistic models that attempt to capture system dynamics and complexity. This trend has been supported (and perhaps encouraged) by the availability of suitable computer plat-

forms capable of processing the immense amount of information required to simulate these processes, as well as the availability of suitable covariate data.

The need for a more rapid response in outbreak situations has resulted in the recent development of fine-scale dispersal models designed to forecast and backcast spread for surveillance and response activities (Guichard et al. 2012) and generic models, such as a General Model of Biological Invasions (GMBI) (Renton et al. 2011, Savage et al. in press), Modular Dispersal in GIS (MDiG) (Pitt et al. 2009, 2011), demoniche (Nenzén et al. 2012) and a model suite for Pest Risk Analysis (Robinet et al. 2012). In the future, we anticipate modelling methods will continue to improve our ability to incorporate complex spatial and temporal dynamics, such as highly mechanistic models of wind dispersal. For example, recent research has simulated seed dispersal using a ballistic method coupled with large-eddy simulations incorporating turbulent airflow (Nathan et al. 2011). As sophisticated, multi-level wind circulation models are improved and made more accessible for a wider range of applications (e.g. NCEP/NCAR reanalysis data (NOAA 2011)), the opportunity to couple mechanistic dispersal models with process-based population dynamics models becomes apparent (Parry et al. 2011).

However, even when armed with limitless computing power and knowledge of a species' dispersal ecology we cannot forecast far into the future with high precision. We should be wary therefore of applying increasingly sophisticated mechanistic models and running them for long-term forecasts; the results may appear to have a fine resolution, but this should not be confused with reality – in such instances an analytical approach may be preferable, where fewer variables, constrained behaviour and obvious lack of precision make more explicit the model uncertainties and inaccuracies. Overall, there is great value in combining modelling methods; indeed it is likely to be necessary as the multi-dimensionality of the problem of post-entry pest spread will often require an integrated, multi-model, multi-scale approach, aligned with an empirical surveillance programme.

The most pressing limitations to applying spread modelling to post-entry invasion ecology are clearly not methodological. Modellers are spoilt for choice. The biggest constraints concern our knowledge of the rates of spread of organisms in novel landscapes at fine spatial and temporal scales, as well as across the time course of invasions. A clear challenge here is the cost of monitoring the spread of invasive organisms, which typically sees a rapid decline in interest once an organism stops being an eradication target. Options for overcoming this problem include placing more emphasis on the collection of time-stamped location data for invasive species, "crowd-sourcing" initiatives, and the development of a rich library of spread rate data for different organisms.

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